

# ALYTES

INTERNATIONAL JOURNAL OF BATRACHOLOGY

March 1996

Volume 13, N° 4

*Alytes*, 1996, 13 (4): 109-139.

109

## Comparative morphology of phytotelmonous and pond-dwelling larvae of four neotropical treefrog species (Anura, Hylidae, *Osteocephalus oophagus*, *Osteocephalus taurinus*, *Phrynohyas resinifictrix*, *Phrynohyas venulosa*)

Luis C. SCHIESARI \*, Britta GRILLITSCH \*\* & Claus VOGL \*\*

\* Departamento de Zoologia, Instituto de Biociências, Universidade de São Paulo, CP 11294, 05422-970, São Paulo, SP, Brasil  
leschies@usp.br

\*\* Institute of Laboratory Animal Science, University of Veterinary Medicine of Vienna, Linke Bahngasse 11, 1030, Vienna, Austria  
brittagr@ping.at

We dedicate this paper to the memory of Rudolf WYTEK († August 25, 1995, Vienna)

**External and buccopharyngeal morphology of phytotelmonous and pond-dwelling larvae of four neotropical hylid species were analyzed with respect to differential diagnosis and ecomorphology. Larvae typically live in bromeliads (*Osteocephalus oophagus*), tree holes (*Phrynohyas resinifictrix*), ponds in rainforest (*Osteocephalus taurinus*), and ponds in open areas (*Phrynohyas venulosa*). Discriminant analysis of morphometric external characters revealed only slight differences between the phytotelmonous species, but two well separated subgroups among the pond-dwelling species. All species showed average body proportions, macrophagous habits, and pulmonary as well as branchial respiration. Tadpoles living in phytotelms were characterized by reduction of peribuccal and buccopharyngeal structures, and differed notably in jaw sheath morphology and lung development among species. Tadpoles developing in ponds were characterized by high numbers of tooth rows and low balance values. The genera *Osteocephalus* and *Phrynohyas* were distinguished best by development of secondary upper tooth rows, position of the eyes, and gross body proportions.**



Bibliothèque Centrale Muséum



3 3001 0011593 5

## INTRODUCTION

In this study we describe the tadpoles of *Osteocephalus oophagus* Jungfer & Schiesari, 1995, *Osteocephalus taurinus* Steindachner, 1862, *Phrynohyas resinificatrix* (Goeldi, 1907), and *Phrynohyas venulosa* (Laurenti, 1768). Larval gross body characters and external buccal features are examined through series comprising almost the entire larval period. Internal buccopharyngeal surface features and detailed morphometry are considered in advanced tadpole stages only.

Tadpoles of the four species have already been described by a number of authors (Table I). However, with the exception of *P. venulosa*, those descriptions were based on small samples and provided little information on ontogenetic and intraspecific variation. Information on buccopharyngeal larval morphology was available only for *P. resinificatrix*.

The neotropical hylid genera *Osteocephalus* Steindachner, 1862 (seven species; JUNGFER & SCHIESARI, 1995) and *Phrynohyas* Fitzinger, 1843 (five species; FROST, 1985) are well defined by their adult morphology (TRUEB, 1970; TRUEB & DUELLMAN, 1971). Within both genera, larval habitats vary significantly among species and include phytotelms, ponds, and streams (Table VIII). The larval habitats for the four species in this study are principally of two types: phytotelms and ponds. Larvae of *O. oophagus* typically develop in rainforest bromeliads at the ground or off-ground up to 2 m high; those of *P. resinificatrix* dwell in spacious tree holes in the canopy up to 35 m high. In contrast, larvae of *O. taurinus* typically develop in rainforest ponds and those of *P. venulosa* in ponds of open areas.

To better understand larval morphology of the species analyzed in depth in this study, we finally include comparative data from the literature on other *Osteocephalus* and *Phrynohyas* species (Table VIII, fig. 7) and refer to phenotype-ecotype interdependencies recognized for anuran larvae (WASSERSUG, 1980; LANNON et al., 1987; WASSERSUG & HEYER, 1988; ALTIG & JOHNSTON, 1989).

## MATERIAL AND METHODS

Collection data, as well as the number and range of developmental stages of the tadpoles examined, are summarized in Table II. Tadpoles were preserved in 4% formaldehyde solution. Most of the series were preserved in the field shortly after collection. Some series of *P. resinificatrix* and *O. taurinus* were reared in the laboratory from spawn or tadpoles collected in the field. Specific assignment of the tadpoles collected by L. C. SCHIESARI was confirmed by specimens raised in the laboratory either from identified spawn or until neometamorphosed stages (exceeding stage 46, GOSNER, 1960), and was confirmed by congruency with the museum tadpole series indicated in Table II. *P. venulosa* larvae were identified by J. P. CALDWELL.

Determination of larval developmental stages follows GOSNER (1960). Morphometric parameters (Table III) are defined as in GRILLITSCH et al. (1993). Within stages, the

Table I. - Literature survey on larval morphology of *Osteocephalus oophagus*, *Osteocephalus taurinus*, *Phrynohyas resinifictrix* and *Phrynohyas venulosa*. Information present (+) or not present (-).

Species	Stages	Localities	Features							References
			General appearance		Oral disk		Buccopharyngeal cavity		Morphometry	
			Described	Illustrated	Described	Illustrated	Described	Illustrated		
<i>O. oophagus</i>	37	Manaus, Amazonas, Brasil	-	+	-	-	-	-	-	HERO (1990) <sup>1</sup>
	19-40	Manaus, Amazonas, Brasil	+	+	+	-	-	-	+	JUNGFER & SCHIESARI (1995)
<i>O. taurinus</i> <sup>2</sup>	40-41	Manaus, Amazonas, Brasil	-	+	-	+	-	-	-	HERO (1990)
<i>P. resinifictrix</i>	-	-	+	-	+	-	-	-	-	LANNOO et al. (1987)
	39	Manaus, Amazonas, Brasil	-	+	-	+	-	-	-	HERO (1990)
	28-38	Panguana, Perú	+	+	+	+	+	+	+	GRILLITSCH (1992)
<i>P. venulosa</i>	18-41	Bejuco, Panamá, Panamá	+	+	+	+	-	-	+	ZWEIFEL (1964)
	17-46	Encinal, Veracruz, México	+	+	+	+	-	-	+	PYBURN (1967) <sup>3</sup>
	38	Encinal, Veracruz, México	+	+	+	+	-	-	-	DUELLMAN (1970) <sup>4</sup>
	38	Leticia, Colombia	+	-	+	-	-	-	-	DUELLMAN (1978)
		Río Negro, Edo. Miranda, Venezuela	+	+	+	+	-	-	-	RADA DE MARTINEZ (1990)

1. Tadpoles described under the name *Osteocephalus* sp.

2. Description of *O. taurinus* tadpoles in DUELLMAN & LESCURE (1973) must be referred to *Hyla geographica* (CALDWELL, 1989); this also applies to the *O. taurinus* tadpole described in DUELLMAN (1978). Original description of *Hyla elkejungingerae* (HENLE, 1981) includes larval morphology. This species has been considered a possible synonym of *O. taurinus* (FROST, 1985), but was redefined by HENLE (1992) as *Osteocephalus elkejungingerae* and is considered as a distinct species in the present study.

3. Tadpoles described under the name *Phrynohyas spilomma*.

4. Reexamination of the series of ZWEIFEL (1964) and PYBURN (1967), and comparison with a further series from Tepic, Nayarit (México), support conspecificity of the tadpoles of ZWEIFEL and PYBURN.

Table II. - Material investigated: Museu Nacional do Rio de Janeiro, Brasil (MNRJ); Museu de Zoologia da Universidade de São Paulo, Brasil (MZUSP); L. C. SCHIESARI field numbers of material deposited in the MZUSP (LCS).

Localities: Reserva Florestal Adolfo Ducke, Manaus, Amazonas, Brasil (A); Reservas INPA No. 3402, 1501, 1401, Instituto Nacional de Pesquisa do Amazonas - World Wildlife Fund, Amazonas, Brasil (B); Juruá, Rio Xingú, Pará, Brasil (C); Boa Vista, Roraima, Brasil (D).

Collectors: see notes.

Morphometry: number of specimens and range of stages of the specimens investigated for gross body morphometry (Table III), detailed morphometry (Table III) and tooth row counts (Table IV).

Specimen series	Localities (collectors)	Dates of collections	Gross morphometry		Detailed morphometry		Tooth row counts	
			Numbers of specimens	Ranges of stages	Numbers of specimens	Ranges of stages	Numbers of specimens	Ranges of stages
<i>O. oophagus</i>	A <sup>4</sup>							
LCS 345		26.01.93	7	27-37	7	37-39	8	27-37
LCS 361 <sup>1,2,3</sup>		09.03.93	20	31-40	1	37	17	31-40
<i>O. taurinus</i>								
MNRJ 7971 <sup>1,2</sup>	A <sup>5</sup>	26.10.85	6	35-39	3	37-39	6	35-39
MZUSP 66336	B <sup>6</sup>	01.-05.93	3	36-39	2	39	3	36-39
LCS 343 <sup>3</sup>	A <sup>4</sup>	27.01.93	33	25-26	-	-	34	25-26
LCS 364 <sup>3</sup>	A <sup>4</sup>	12.03.93	17	27-28	-	-	16	27-28
<i>P. resinifictrix</i>	A <sup>4</sup>							
LCS 342 <sup>3</sup>	Tree 1	21.01.-11.03.93	6	30-36	-	-	5	30-36
LCS 355	Tree 1	18.02.93	9	25-26	-	-	4	25-26
LCS 362	Tree 1	10.03.93	2	25	-	-	2	25
LCS 372-375 <sup>1</sup>	Tree 1	13.02-12.06.93	30	25-40	3	37	19	26-41
LCS 347	Tree 2	28.01.93	8	26-35	-	-	7	26-35
LCS 356	Tree 2	18.02.93	6	27-31	-	-	4	27-30
LCS 376-377 <sup>2</sup>	Tree 2	29.01.-17.04.91	17	25-39	3	37-39	16	25-39
LCS 378 <sup>1</sup>	Tree 3	29.01.91	14	25-37	1	37	12	26-37
LCS 366	Tree 4	18.03.93	2	25	-	-	2	25
LCS 379	Tree 5	30.01.91	5	25	-	-	4	25
LCS 357 <sup>3</sup>	Tree 6	24.02-09.03.93	8	27-37	2	37	8	27-37
<i>P. venulosa</i>	C <sup>7</sup>							
MZUSP 64359		15.01.87	5	30-34	-	-	5	20-34
MZUSP 64360 <sup>1</sup>		1987	2	35-37	1	37	2	35-37
MZUSP 64361 <sup>1,2</sup>		27.01.87	4	37-40	3	37-38	-	-
MZUSP 64364		05.02.87	1	39	2	39	-	-
MZUSP 64367		14.02.87	2	25	-	-	3	25
MZUSP 68933	D <sup>7</sup>	23.06.91	2	36-37	1	37	2	36-37

1. Samples used for SEM analysis of buccopharyngeal cavity.

2. Samples used for SEM analysis of oral disk.

3. Samples raised in the laboratory.

4. Coll. L. C. SCHIESARI.

5. Coll. J.-M. HERO.

6. Coll. C. GASCON.

7. Coll. J. P. CALDWELL.

Table III. - Comparison of morphometric parameters describing the body proportions of the tadpoles of *Osteocephalus oophagus*, *Osteocephalus taurinus*, *Phrynohyas resinifictrix* and *Phrynohyas venulosa*, for developmental stages pooled within two different ranges.

Parameters (distances as defined in GRILLITSCH et al., 1993): maximum diameter of eye (ED); maximum height of tail (HT); maximum height of lower tail fin (LF); internarial distance (NN); nairo-pupillar distance (NP); maximum width of oral disk (OD); interpupillar distance (PP); rostro-narial distance (RN); distance tip of snout - opening of spiracle (SS); distance tip of snout - insertion of upper tail fin (SU); distance snout - vent, snout-vent length (SV); maximum height of upper tail fin (UF); distance vent - opening of spiracle (VS); distance vent - tip of tail, tail length (VT).

For each parameter, the following information is provided: mean value  $\pm$  standard deviation; range in parenthesis; number of specimens in brackets; coefficient of regression of ratios with total length / Spearman correlation coefficient of ratios with stage in waved brackets, \*  $P < 0.05$ , \*\*  $P < 0.01$ .

Parameters		Stages pooled	<i>O. oophagus</i>	<i>O. taurinus</i>	<i>P. resinifictrix</i>	<i>P. venulosa</i>
Vent - tail tip / snout - vent	VT / SV	26 - 40	1.20 $\pm$ 0.13 (0.82-1.47) [27] {0.0000/-0.25}	1.36 $\pm$ 0.08 (1.22-1.52) [35] {0.0017/0.01}	1.47 $\pm$ 0.11 (1.25-1.72) [87] {-0.0030/0.12}	1.38 $\pm$ 0.08 (1.26-1.50) [14] {0.0061/0.41}
		36 - 40	1.17 $\pm$ 0.14 (0.82-1.41) [12]	1.38 $\pm$ 0.09 (1.22-1.49) [7]	1.47 $\pm$ 0.12 (1.25-1.70) [18]	1.41 $\pm$ 0.08 (1.26-1.50) [8]
Vent - tail tip / tail height	VT / HT	26 - 40	2.42 $\pm$ 0.26 (1.99-3.07) [23] {0.0216/0.05}	3.26 $\pm$ 0.29 (2.77-4.23) [30] {0.0075/-0.01}	2.53 $\pm$ 0.26 (2.06-3.05) [47] {0.0070/0.16}	2.50 $\pm$ 0.18 (2.14-2.75) [14] {-0.0111/-0.32}
		36 - 40	2.47 $\pm$ 0.31 (2.04-3.07) [10]	3.60 $\pm$ 0.34 (3.20-4.23) [5]	2.55 $\pm$ 0.12 (2.34-2.83) [12]	2.44 $\pm$ 0.18 (2.14-2.69) [8]
Tail height / upper fin height	HT / UF	26 - 40	3.15 $\pm$ 0.15 (2.90-3.41) [24] {0.0025/0.26}	3.44 $\pm$ 0.28 (3.05-4.21) [30] {0.0074/-0.31 *}	3.10 $\pm$ 0.29 (2.71-3.71) [50] {0.0329 **/0.15}	2.84 $\pm$ 0.11 (2.63-3.03) [16] {0.0023/-0.02}
		36 - 40	3.19 $\pm$ 0.14 (2.94-3.41) [10]	3.63 $\pm$ 0.39 (3.06-4.21) [5]	3.07 $\pm$ 0.25 (2.74-3.56) [13]	2.82 $\pm$ 0.10 (2.63-2.94) [9]
Upper fin height / lower fin height	UF / LF	26 - 40	1.07 $\pm$ 0.07 (0.92-1.19) [24] {0.0085 **/0.48 **}	1.03 $\pm$ 0.09 (0.79-1.16) [30] {0.0039 */0.18}	0.99 $\pm$ 0.09 (0.79-1.16) [50] {0.0023/0.35 **}	0.98 $\pm$ 0.06 (0.86-1.10) [16] {-0.0033/-0.16}
		36 - 40	1.10 $\pm$ 0.06 (0.99-1.19) [10]	1.11 $\pm$ 0.07 (0.99-1.22) [5]	1.02 $\pm$ 0.08 (0.90-1.16) [13]	0.97 $\pm$ 0.05 (0.86-1.04) [9]
Snout - vent / snout - upper fin	SV / SU	26 - 40	1.66 $\pm$ 0.15 (1.32-2.15) [27] {-0.0063/-0.17}	1.51 $\pm$ 0.08 (1.37-1.71) [31] {0.0000/0.11}	1.65 $\pm$ 0.20 (1.36-2.19) [50] {0.0062/0.22}	2.07 $\pm$ 0.20 (1.81-2.39) [15] {0.0079/0.22}
		36 - 40	1.65 $\pm$ 0.19 (1.32-2.15) [12]	1.50 $\pm$ 0.09 (1.44-1.66) [4]	1.72 $\pm$ 0.18 (1.42-1.93) [13]	2.16 $\pm$ 0.22 (1.84-2.39) [8]
Snout - spiracle / vent - spiracle	SS / VS	36 - 40	1.20 $\pm$ 0.15 (0.98-1.49) [8]	1.23 $\pm$ 0.17 (0.94-1.46) [5]	1.18 $\pm$ 0.15 (0.94-1.41) [9]	1.35 $\pm$ 0.16 (1.12-1.64) [7]
Interpupillar / internarial	PP / NN	36 - 40	1.51 $\pm$ 0.05 (1.43-1.59) [8]	1.42 $\pm$ 0.06 (1.36-1.51) [5]	1.67 $\pm$ 0.07 (1.51-1.75) [9]	1.51 $\pm$ 0.04 (1.45-1.58) [7]
Rostro-narial / nairo-pupillar	RN / NP	36 - 40	1.03 $\pm$ 0.10 (0.85-1.20) [8]	0.92 $\pm$ 0.14 (0.73-1.15) [5]	0.78 $\pm$ 0.15 (0.53-1.13) [9]	0.86 $\pm$ 0.15 (0.63-1.04) [7]
Interpupillar / oral disk width	PP / OD	36 - 40	1.61 $\pm$ 0.06 (1.55-1.74) [8]	1.51 $\pm$ 0.09 (1.36-1.62) [5]	2.24 $\pm$ 0.12 (2.09-2.43) [9]	1.87 $\pm$ 0.06 (1.81-1.96) [6]
Internarial / oral disk width	NN / OD	36 - 40	1.07 $\pm$ 0.04 (1.03-1.15) [8]	1.06 $\pm$ 0.07 (0.99-1.16) [5]	1.34 $\pm$ 0.08 (1.22-1.45) [9]	1.25 $\pm$ 0.03 (1.21-1.28) [6]
Interpupillar / eye diameter	PP / ED	36 - 40	3.24 $\pm$ 0.26 (2.92-3.63) [8]	3.15 $\pm$ 0.22 (2.88-3.49) [5]	4.17 $\pm$ 0.42 (3.54-4.85) [9]	3.92 $\pm$ 0.07 (3.78-3.99) [7]

Table IV. - Comparison of collective median formulae (DUBOIS, 1995) of labial tooth rows (median values, range in parentheses, number of specimens in brackets, presence and position of gaps not indicated) of *Osteocephalus oophagus*, *Osteocephalus taurinus*, *Phrynohyas resinifictrix* and *Phrynohyas venulosa*, in relation to the stage of larval development.

Stages	Median collective tooth row formulae							
	<i>O. oophagus</i>		<i>O. taurinus</i>		<i>P. resinifictrix</i>		<i>P. venulosa</i>	
25	-		2 / 3 (3-4)	[27]	2 / 3 (3-4)	[15]	2 / 3	[3]
26	-		2 / 4 (3-4)	[10]	2 / 3;4 (3-4)	[16]	-	
27	2 / 3	[1]	2 / 5	[5]	2 / 4 (3-4)	[11]	-	
28	2 / 3	[1]	2 / 5 (5-6)	[11]	2 / 4	[5]	-	
29	2 / 3	[1]	-		2 / 4 (3-4)	[3]	-	
30	2 / 3	[1]	-		2 / 4 (3-5)	[6]	3 / 4	[1]
31	2 / 3	[3]	-		2 / 4 (3-4)	[6]	3 / 4	[3]
32	-		-		2 / 5	[1]	-	
33	2 / 3	[2]	-		2 / 4	[2]	-	
34	2 / 3	[2]	-		2 / 4 (3-4)	[3]	3 / 5	[1]
35	2 / 3	[3]	2 / 6	[1]	2 / 4	[2]	3 / 5	[1]
36	2 / 3	[1]	2 / 5 (4-6)	[3]	2 / 4	[4]	4 / 5	[1]
37	2 / 3	[2]	2 / 7;6 (6-7)	[2]	2 / 4	[8]	3 / 5 (4-5)	[4]
38	2 / 3	[3]	-		-		3 / 4	[1]
39	2 / 3	[4]	2 / 6 (5-6)	[3]	2 / 4 (3-4)	[3]	3 / 5	[2]
40	2 / 3	[1]	-		2 / 4	[4]	3 / 5	[1]
41	-		-		2 / 4	[1]	-	

collective labial tooth row formula (DUBOIS, 1995) is described by median value and range of tooth row counts in the anterior and posterior labium, respectively. Balance values of tooth row counts (i.e., number of rows in the upper labium minus number of rows in the lower labium) are according to ALTIG & JOHNSTON (1989), who categorized tooth row formulae as balanced (equal number of rows on upper and lower labia), negatively imbalanced (more rows on lower labium), or positively imbalanced (more rows on upper labium). Terminology of jaw sheath morphology follows, e.g., KAUNG & KOLLROS (1976) and FOX (1984). Terminology of buccopharyngeal structures is in accordance with WASSERSUG (1976, 1980) and WASSERSUG & HEYER (1988). Typological assignment of breeding habitats (Table VIII) corresponds to DUELLMAN & TRUEB (1985), LANNOO et al. (1987), DUELLMAN (1988), and ALTIG & JOHNSTON (1989).

The tadpoles analyzed comprise a wide range of developmental stages (Table II). For all specimens, developmental stage, total length (fig. 1), gross body proportions (Table III), and tooth row counts (Table IV) were determined. Investigations on further morphometric parameters (Tables III and V) and on buccopharyngeal structures were

Table V. - Comparison of (A) external and (B) internal features of *Osteocephalus oophagus*, *Osteocephalus taurinus*, *Phrynohyas resinifictrix* and *Phrynohyas venulosa* in advanced larval developmental stages ( $38 \pm 2$ , numbers of specimens according to those in Tables II and IV).

## A. External features.

Parameters	<i>O. oophagus</i>	<i>O. taurinus</i>	<i>P. resinifictrix</i>	<i>P. venulosa</i>
Mean total length (mm)	29.7	32.7	37.0	41.8
Maximum total length (mm, present study)	36.2 (stage 40)	38.3 (stage 39)	47.0 (stage 39)	39.9 (stage 39)
Maximum total length (mm, from the literature) <sup>1</sup>	26.0 (stage 37)	31.7 (stage 40)	38.7 (stage 39)	49.4 (stage 41)
Labial tooth row formula (present study) <sup>2</sup>	2 / 3	2 / 6 (4-7)	2 / 4 (3-4)	3 (3-4) / 5 (4-5)
Labial tooth row formula (from the literature) <sup>1,2</sup>	2 / 3	2 / 6 (4-7)	2 / 4 (3-4)	3 (3-4) / 5 (4-7)
Total number of labial papillae <sup>2</sup>	98;100 (88-114)	160 (146-162)	120 (90-144)	168;182 (150-210)
Number of labial papillae per 100 $\mu\text{m}^3$	1.5-2	2	2	1.5
Height of exposed part of apical cone cells ( $\mu\text{m}$ ) <sup>4</sup>	10-12	21-27	35-47	27-32
Number of apical cone cells per 100 $\mu\text{m}^4$	10	6-7	6-7	6-7
Number of labial keratodonts per 100 $\mu\text{m}^5$	10-14	10-13	6-9	9-12
Number of keratodont serrations <sup>5</sup>	8-10	10-12	12-14	14-16

## B. Internal features.

Parameters	<i>O. oophagus</i>	<i>O. taurinus</i>	<i>P. resinifictrix</i>	<i>P. venulosa</i>
Total number of postnarial papillae	3-4	3-4	3-4	3-4
Number of lateral ridge papillae per side	1	1	1	1
Number of buccal roof arena papillae per side <sup>6</sup>	(30-45)	40-50	(25-35)	50-60
Diameter of secretory pits in dorsal velar glandular zone ( $\mu\text{m}$ )	15-20	15-20	5-15	10-25
Angle between longitudinal axis of nares and transversal body axis	40°-45°	40°-45°	30°-45°	10°-20°
Number of praelingual palps per side	1	1	1	1
Total number of lingual papillae	2	2	2	2
Number of marginal buccal floor arena papillae per side	3-6	11-16	6-10	10-15
Number of central buccal floor arena papillae per side <sup>6</sup>	(13-15)	13-15	(0-3)	12-14
Diameter of secretory pits in ventral velar glandular zone ( $\mu\text{m}$ )	20-30	15-30	5-10	15-40
Folding pattern of filter rows <sup>7</sup>	2° [3°]	3° (4°)	2° (3°)	4°
Branching pattern of gills <sup>8</sup>	3°	3°	2°	3°
Length of gill tufts ( $\mu\text{m}$ ) <sup>8</sup>	350-400	400-500	300-350	450-650
Extension of lungs <sup>9</sup>	1/2	2/3	3/4	3/4

1. References according to Table I.

2. Median values, ranges in parentheses.

3. In ventromedian position on oral disk.

4. In median position on upper jaw sheath.

5. In median position on continuous upper tooth row.

6. Indistinctly developed papillae in parentheses.

7. Secondary, tertiary, quaternary, features found in some cases in parentheses, found exceptionally in brackets.

8. In median position on second ceratobranchial.

9. Mean maximum caudal extension of inflated lungs in the abdominal cavity.

restricted to specimens of stages  $38 \pm 2$ . We excluded material below developmental stage 26 from subsequent statistical analysis because of small sample sizes.

For examination of buccopharyngeal features, scanning electron microscopy (SEM, two specimens per species) and stereo light microscopy (methylene blue staining, three specimens per species) were used. Data on external features were based on stereo microscopic examination. Oral disk structures were confirmed by SEM (two specimens per species). Preparation for SEM examination (Jeol JSM-35 CF) followed a standard procedure (ethanol dehydration, critical-point-drying, gold sputter surface-coating). Measurements were determined using a digital display length-measuring unit (Wild MMS 235) attached to a stereo microscope (Wild M8).

For statistical analyses, SPSS for Windows (Version N° 5.0.2.) was used. Gross body proportions were described by basic descriptive statistics. Since material examined included a wide range of developmental stages, we tested for covariation of ratios (Table III) with total length (univariate regression for each species) and correlation of ratios with stage (Spearman rank correlation), as well as for isometry of growth. Gross body measures were log-transformed and regressed against total length ( $\ln y = \ln a + b \ln x$ ; GOULD, 1966). Where the regression coefficient ( $b$ ) was significantly different from 1.0, the isometry hypothesis ( $H_0$ ) was rejected. We also estimated the regression of the ratios describing the gross body proportions on total length.

With discriminant analysis, we estimated the optimum linear combination of variables for differential diagnosis and the probability of misclassification of individuals. We used the ratios of gross body proportions for these analyses and included the number of upper and lower tooth rows. The latter two are meristic characters, and number of upper tooth rows did not show any variation in three of the species studied. Therefore, some within group variance-covariance matrices were singular. Discriminant analysis is fairly robust against this type of violation of assumptions, and, as an exploratory tool, provided concise results.

To estimate the relative influences of phylogenetic relationship (genus) and contemporary larval habitat (ecotype), univariate as well as multivariable analyses of covariance (ANCOVA, MANCOVA) were performed (stages  $38 \pm 2$ ). The dependent variables were logarithms of absolute gross body measures and of numbers of upper and lower tooth rows. A full factorial mixed model was used with ecotype (phytotelm versus pond) and genus (*Osteocephalus* versus *Phrynohyas*) as factors and total length as covariate (JOHNSON & WICHERN, 1988; MORRISON, 1990).

For the material examined, each ecotype was represented in each genus, hence, all cells of the model were occupied. However, the number of individuals in each cell was unbalanced, and the individual sums of squares did not add up to the total sum of squares in the ANCOVA. Since our design is "not extremely unbalanced" (SHAW, 1987), results are not substantively compromised, and the application of other estimators will compare to the ANOVA estimator (SWALLOW & MONAHAN, 1984; SHAW, 1987).



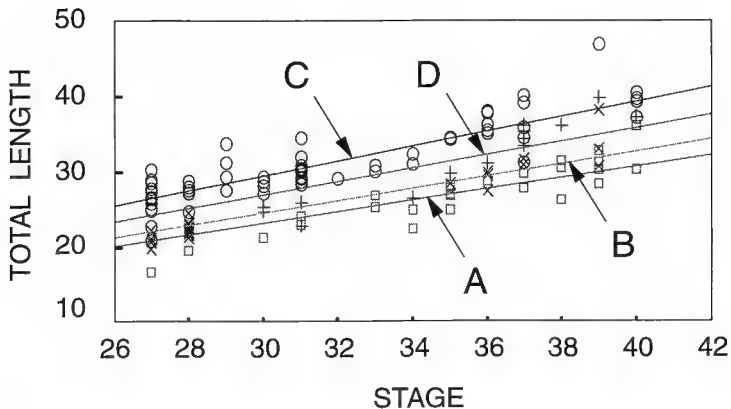


Fig 1 - Size-stage graphs (scatter plots, regression lines) of developmental stages (GOSNER, 1960) and total lengths (mm): *Osteocephalus oophagus* (A, squares), *Osteocephalus taurinus* (B, multiplication signs); *Phrynohyas resinifictrix* (C, circles); *Phrynohyas venulosa* (D, addition signs).

## RESULTS

For complete and concise description, presentation of results is based on the following conventions:

(1) Descriptions apply to all four species where no interspecific differences are indicated.

(2) Relative descriptive terms without quantification or reference of comparison refer to external morphology of "generalized pond-type hyloid larvae" (DUELLMAN, 1970) and to the terminology for the description of buccopharyngeal morphology as used by, e.g., WASSERSUG (1980), VIERTTEL (1982), INGER (1985), and WASSERSUG & HEYER (1988).

(3) Precise values of the ratios describing body proportions and corresponding abbreviations are presented in Table III, metric and meristic values of oral disk and buccopharyngeal features in Table V.

For stages 26 through 40, almost all ratios describing gross body proportions covaried with neither total length nor stage (Table III), and therefore were pooled, in addition to the presentation for tadpoles in advanced developmental stages ( $38 \pm 2$ ). In test for isometry, the regression coefficients did not differ significantly from 1.0, i.e., tadpoles' growth was isometric from stage 26 on in all gross body measures, except for tail height in *O. oophagus* and *P. resinificatrix*. In these species, the tail height grew proportionately less than total length.

Through all stages examined, mean total length increased from *O. oophagus*, through *O. taurinus* and *P. venulosa*, to *P. resinificatrix* (fig. 1).

## GENERAL DESCRIPTION

Body slightly depressed; in dorsal view, elongate elliptical in *P. venulosa*, elongate ovoid in *O. taurinus*, round ovoid to piriform in *O. oophagus*, elongate elliptical to piriform in *P. resinificatrix*. In *P. resinificatrix*, *O. oophagus* and *O. taurinus*, body width correlated with amount of ingested eggs. Those eggs were visible through the abdominal wall, notably in *O. oophagus*, whose integument was comparatively pale, thin and transparent.

Spiracular tube sinistral, directed posterodorsally, tightly attached to the body, opening slightly below midline of body, at about one-half to two-thirds of distance from tip of snout to opening of vent tube (SS/SV). Vent tube of moderate size, opening medially to subdextrally at edge of ventral fin. Tail length equal to three-halves the snout-vent length; tail proportionately shortest in *O. oophagus* and longest in *P. resinificatrix* (VT/SV). Dorsal tail fin extending moderately onto body, inserting one-half to two-thirds the snout-vent length distant from tip of snout; insertion of dorsal tail fin most anterior in *P. venulosa* (SV/SU). Tail length twice to four times the tail height; tail height three to four times the height of dorsal tail fin; *O. taurinus* with least maximum tail height in relation to tail length and shallowest upper tail fin compared to the maximum height of tail (VT/HT, HT/UF). Fin edges arched, compared to the margins of caudal musculature,

more convex in *P. venulosa* than in *P. resinifictrix*, fairly parallel in *Osteocephalus*. Upper and lower fins almost equally high (UF/LF), gradually tapering. Caudal musculature moderate, nearly reaching the obtusely pointed tip of tail.

In dorsal view, snout nearly truncate in *O. oophagus*, bluntly rounded in the other species. In lateral profile, snout acutely rounded in *O. oophagus*, rounded in *P. resinifictrix* and *P. venulosa*, bluntly rounded in *O. taurinus*. Oral disk subterminal; position correlated with shape of snout (Table V.A); most anterior and, if expanded, partly visible in dorsal view in *O. oophagus*, and increasingly more posterior from *P. resinifictrix* through *P. venulosa* to *O. taurinus*. Eyes moderately large, situated dorsolaterally; widely spaced, directed laterally, visible in ventral view in *Phrynohyas*, slightly less separated, directed dorsolaterally, not visible in ventral view in *Osteocephalus*. Nostrils rimmed, directed anterolaterally, about midway between pupillae and tip of snout in *Osteocephalus*, slightly more anterior in *Phrynohyas* (RN/NP), internarial distance about two-thirds the interpupillar distance (PP/NN).

#### ORAL DISK

Oral disk (fig. 2) medium-sized, moderately expanded laterally, slightly trilobate ventrally. Labial papillae average sized; extension of dorsomedian gap about one-fifth of continuous upper tooth row in *O. oophagus*, *P. resinifictrix* and *P. venulosa*, one-third of continuous upper tooth row in *O. taurinus*. In the fully expanded oral disk, marginal labial papillae arranged in a single or alternating double row; submarginal papillae scattered in the lateral oral disk portions, most frequently ventrolaterally, often in lateral continuation of the outermost lower tooth rows. Labial papillae more numerous in *P. venulosa* and *O. taurinus* than in *P. resinifictrix* and *O. oophagus* (Table V.A); denticulate papillae in the lateral portions of the oral disk and in lateral extension of secondary tooth rows frequently present in *P. venulosa*, exceptionally present in *P. resinifictrix*.

In early larval stages, two upper and three lower labial tooth rows present (Table IV, fig. 7). Labial tooth row formula 2/3 retained throughout entire larval period in *O. oophagus*, and occasionally in advanced stages in *P. resinifictrix*; in the other species, additional lower tooth rows appearing with increasing developmental stages (Table IV). One or two additional upper tooth rows developed only in *P. venulosa* (Tables IV and V.A). Maximum total number of tooth rows 5 in *O. oophagus*, 7 in *P. resinifictrix*, 9 in *O. taurinus* and *P. venulosa*.

Morphology of ontogenetically basic upper two and lower three tooth rows quite homogeneous in all species. Outer upper primary row continuous, inner one shortly interrupted medially, with its median ends often covered by the outer tooth row, both coextending far towards the lateral corners of the oral disk. Ridges of lower three primary rows frequently indented medially when not fully expanded; innermost always continuous in *P. resinifictrix*, occasionally with a very narrow median interruption in the other species; outer two always continuous; all three typically of broad and almost equal lateral extension, outermost often shorter than the inner ones in *O. oophagus*.

Tooth rows in excess of the basic 2/3 pattern added centrifugally in the upper (*P. venulosa*) as well as in the lower labium; typically, with broad median interruption in

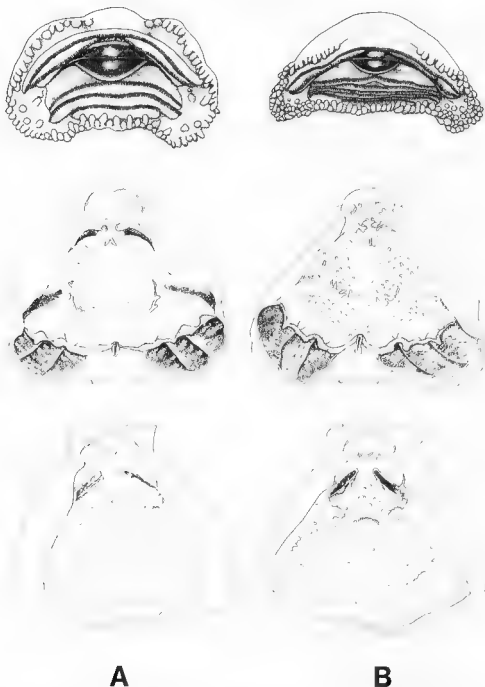
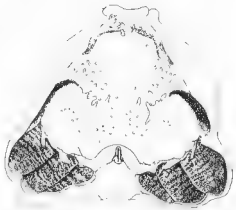
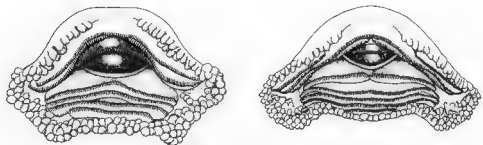


Fig. 2. — Drawings of oral disk (top), floor (middle) and roof (bottom) of buccopharyngeal cavity after SEM micrographs: A, *Osteocephalus oophagus* (1.93/3.87); B, *Osteocephalus taurinus* (2.33/4.94), C, *Phrynohyas resinifictrix* (1.84/5.30); D, *Phrynohyas venulosa* (2.33/4.62). Maxi-

**C****D**

mm horizontal (graph) diameter (in mm) of oral disk / of buccopharyngeal cavity in parentheses. Measures according to SEM micrographs; SEM preparation shrinkage factor about 0.70.

the upper labium (*P. venulosa*), continuous in the lower labium; shorter and more frequently broken the more distally positioned.

Labial keratodonts in a single series on each ridge, cone-shaped with spatulate apical portions bearing acute marginal denticles; size and density of keratodonts, and number of apical indentations slightly varying among species and genera (Table V.A).

Jaw sheaths (fig. 2) broadly dark pigmented, robust, wide, reaching far towards lateral corners of oral disk; front surfaces of average curvature; median part of occlusive margins slightly convex and rectilinear; jaw sheaths moderately narrower and more delicate in *O. oophagus* than in the other species. Edges of upper and lower jaw sheaths smooth in *O. oophagus*, finely serrated in the other species. In SEM examination, exposed parts of apical cone cells incisiform in *O. oophagus*, caniniform in the other species (fig. 3), shape subrectangular with nearly straight distal edges and tight lateral attachment in *O. oophagus*, acutely pointed, cone-shaped in *O. taurinus*, lanceolate in *Phrynohyas*; longest and most acutely tapered in *P. resinifictrix* (Table V.A).

#### BUCCOPHARYNGEAL CAVITY

Buccopharyngeal surface features quite homogeneous in all four species. Variation mainly restricted to number and size of the papilla-derived structures, being longer and more numerous in *O. taurinus* and *P. venulosa* than in *O. oophagus* and *P. resinifictrix*, with *O. oophagus* showing the simplest and *P. venulosa* the most differentiated pattern (Table V.B, fig. 2).

Buccopharyngeal roof. — Prenarial arena broad, centrally with stout tuberosus pustulations, scattered or fused to a median knob or ridge, of variable arrangement even within a species. Internal nares elongate, obliquely oriented; relative length of internal nares in *Phrynohyas* about two-thirds that of *Osteocephalus*; angle between longitudinal axis of internal nares and transversal body axis smaller in *P. venulosa* than in the other species (Table V.B). Anterior narial wall lined by tiny, laterally slightly more elongate papillae; posterior narial wall valve smooth-edged, slightly lobate; narial valve projections faint or slightly lobate. Postnarial papillae arranged in an anteriorly convex arch except for some scattered minor pustulations, well separated from each other in *Osteocephalus*, more basely fused in *Phrynohyas*. One lateral ridge papilla per side, broad-based, palp-like, bearing rather stout or conical pustulations. Median ridge average sized, flap-like; triangular, more slender, elongate, small-based, distant from the lateral ridge papillae, with a pointedly lobed margin in *O. oophagus* and *P. resinifictrix*, semicircular, more stout, broad-based, laterally extended towards the lateral ridge papillae, with the margin tightly bordered by a row of small pustulations in *O. taurinus* and *P. venulosa* (Table V.B). Papillae in the spacious buccal roof arena comparatively small in all species. Papillae bordering the arena more distinct; in the lateral corners of the arena slightly elongate in *O. taurinus* and *P. venulosa*, almost absent in *O. oophagus* and *P. resinifictrix*. Lateral roof papillae scarce but minor pustulations. Dorsal velum continuous across midline with the medial edge bare of papillation. Glandular zone distinct in all species. Width of glandular zone and diameter of secretory pits less in *P. resinifictrix* than in the other species (Table V.B, fig. 2)

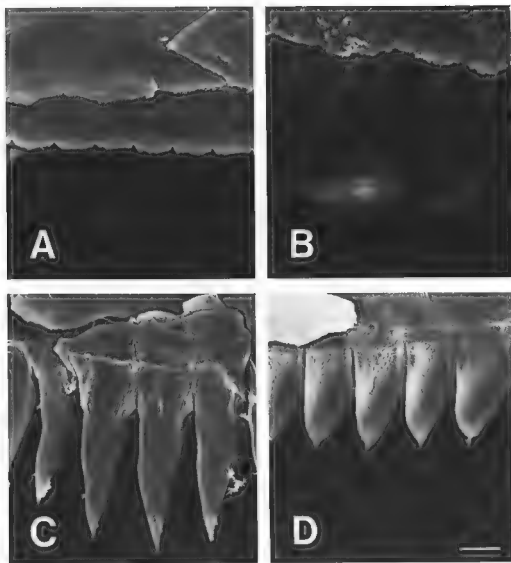


Fig. 3. — SEM micrographs of edge of median upper jaw sheath (scale line equals 10  $\mu$ m): A, *Osteocephalus oophagus*; B, *Osteocephalus taurinus*; C, *Phrynohyas resinifictrix*; D, *Phrynohyas venulosa*

Buccopharyngeal floor. — Prelingual arena scattered with more or less papilliform, stout, laterally and posteriorly more frequent pustulations; almost bare in *O. oophagus*. One average sized, broadly based prelingual palp per side; somewhat larger with the papilliform marginal lobations more elongate, finger-like, and less numerous in *O. oophagus* and *P. resinifictrix* than in the other species. One pair of slim cylindrical lingual papillae. Buccal floor arena well defined, center almost bare; papillae bordering the arena moderately enlarged, conical, simple; lateroposteriorly most distinct and frequently fused basely.

Buccal pockets large; orientation almost transversal in *O. oophagus*, oblique in the other species. Prepocket papillae scarce stout pustulations. Ventral velum distinct with evident spicular support; three spiculae per side. One marginal velar projection per filter cavity; least developed in *O. oophagus*. Free edge of ventral velum lined by a distinct glandular zone; secretory pits largest in *P. venulosa*, slightly smaller in *Osteocephalus*, less prominent in *O. oophagus* than in *O. taurinus*, considerably smaller in *P. resinifictrix* (Table V.B). Branchial food traps with distinct secretory ridges.

Median notch broad, leaving glottis fully exposed; glottal lips broad, elevated; exposure of glottis less distinct in *O. oophagus* than in the other species (fig. 2). Lungs well developed in all species (Table V.B, fig. 5) already in early ectotrophic stages; almost extending to caudal curvature of abdominal cavity except for *O. oophagus* (Table V.B). Esophageal funnel spacious.

Depth of branchial baskets and complexity of the filter rows — i.e., degree of branching (Table V.B), height, depth, and density of filter rows (fig. 4) — decreasing from *P. venulosa* through *O. taurinus* to *P. resinifictrix* and *O. oophagus*. Internal gills least developed in *P. resinifictrix*, next least in *O. oophagus*, most differentiated in *P. venulosa* (Table V.B, fig. 4).

#### DISCRIMINANT ANALYSIS

Discriminant analysis resulted in three, linearly independent, discriminant functions (Table VI). The first discriminant function was dominated by the number of upper tooth rows. The second discriminant function was determined by the ratio of length of tail to height of tail (VT/HT), but was also influenced by the ratio of length of tail to snout-vent length (VT/SV) and the number of tooth rows in the lower labium. The latter two characters also dominated the third and least significant discriminant function. The ratios of height of tail to height of the upper fin (HT/UF), height of the upper fin to height of the lower fin (UF/LF), and of snout-vent length to the distance between tip of snout and insertion of the upper fin (SV/SU) poorly discriminated the species (Table VI.A).

Misclassification of specimens into species was remarkably rare and restricted to the phytotelmonous species (Table VI.B). The group centroid of *P. venulosa* was clearly separated on discriminant function one. On discriminant function two, group centroids were highly positive in *O. taurinus*, while they were negative in *O. oophagus* and *P. resinifictrix*. On the last discriminant function, group centroids of *O. oophagus* and *P. resinifictrix* were distinctly separate. In summary, the phytotelmonous species clustered closely, while the two pond types formed two more separated clusters (Table VI.C, fig. 6).



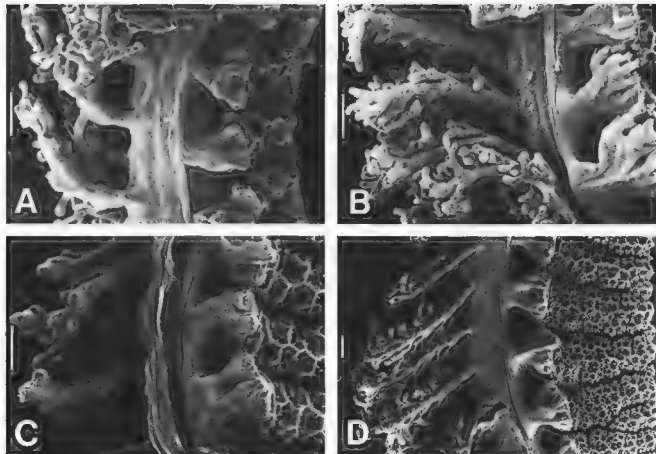


Fig. 4. SEM micrographs of internal gills and filter of median part of second ceratobranchial (scale line equals 100  $\mu$ m): A, *Osteocephalus oophagus*; B, *Osteocephalus taurinus*; C, *Phrynohyas resinifictrix*; D, *Phrynohyas venulosa*.

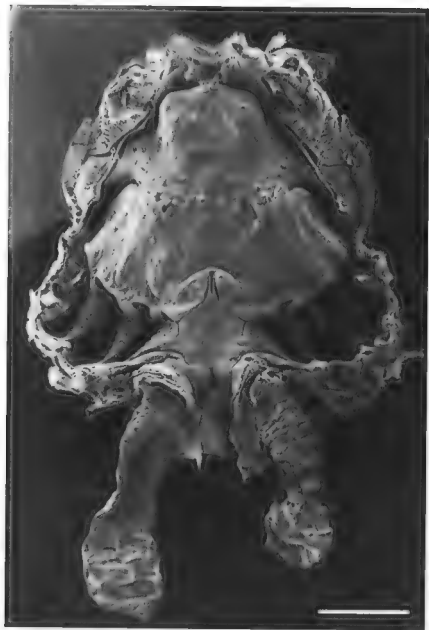


Fig 5. - SEM micrograph of floor of the buccopharyngeal cavity and lung sacs of *Phrynohyas venulosa* (scale line equals 1000  $\mu\text{m}$ )

Table VI. - Discriminant analysis of variables describing gross body proportions (abbreviations according to Table III), including number of tooth rows in the upper and lower labium, for *Osteocephalus oophagus*, *Osteocephalus taurinus*, *Phrynohyas resinifictrix* and *Phrynohyas venulosa* (stages  $38 \pm 2$ ).

A. Coefficients of standardized canonical discriminant functions.

Parameters		Function 1	Function 2	Function 3
Eigenvalues		13.838	3.470	1.576
Vent - tail tip / snout - vent	VT/SV	0.001	-0.602	1.018
Vent - tail tip / tail height	VT/HT	0.103	1.131	-0.265
Tail height / upper fin height	HT/UF	-0.080	-0.209	0.189
Upper fin height / lower fin height	UF/LF	-0.079	-0.203	-0.103
Snout - vent / snout - upper fin	SV/SU	0.080	0.021	-0.012
Number of upper tooth rows	UTR	0.978	-0.010	-0.057
Number of lower tooth rows	LTR	0.075	0.527	0.496

B. Classification of individuals into species (correctly classified individuals on the main diagonal)

Species	Actual numbers of cases	Assigned numbers of cases			
		<i>O. oophagus</i>	<i>O. taurinus</i>	<i>P. resinifictrix</i>	<i>P. venulosa</i>
<i>O. oophagus</i>	20	19	0	1	0
<i>O. taurinus</i>	29	0	29	0	0
<i>P. resinifictrix</i>	43	1	0	42	0
<i>P. venulosa</i>	12	0	0	0	12

C. Canonical discriminant functions at group centroids.

Species	Function 1	Function 2	Function 3
<i>O. oophagus</i>	-1.569	-1.243	-2.320
<i>O. taurinus</i>	-1.094	2.886	0.036
<i>P. resinifictrix</i>	-1.347	-1.319	1.077
<i>P. venulosa</i>	10.090	-0.194	-0.076

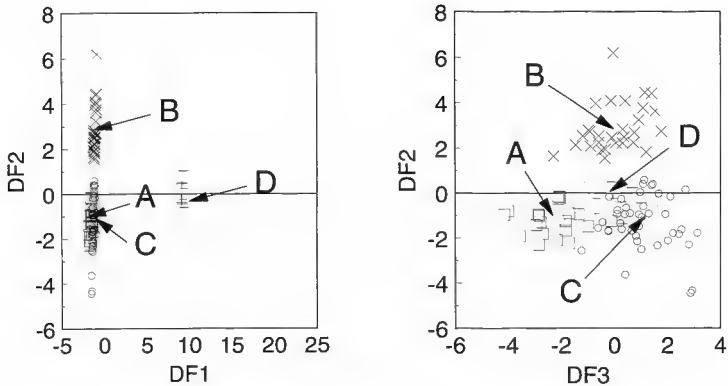


Fig. 6. — Scatter plot of scores of specimens and group centroids (arrows) on discriminant functions (DF) 1 and 2, and 3 and 2: *Osteocephalus oophagus* (A, squares); *Osteocephalus taurinus* (B, multiplication signs); *Phrynohyas resinificatrix* (C, circles); *Phrynohyas venulosa* (D, addition signs).

Table VII. - Analysis of covariance of variables describing gross body proportions (abbreviations according to Table III), including number of tooth rows in the upper and lower labium, for *Osteocephalus oophagus*, *Osteocephalus taurinus*, *Phrynohyas resinificatrix* and *Phrynohyas venulosa* (stages  $38 \pm 2$ ).

ANCOVA: sums of squares (\*  $P < 0.05$ , \*\*  $P < 0.01$ ; individual sums of squares do not sum to total sum, because occupation of cells is unbalanced).

MANCOVA: coefficients of standardized canonical discriminant functions.

Parameters		ANCOVA						MANCOVA			
		Total length	Genus	Ecotype	Interaction	Explained	Residual	Total	Genus	Ecotype	Interaction
Snout - vent	SV	0.16**	0.00	0.02**	0.02**	0.30**	0.08	0.38	0.121	0.378	0.387
Tail height	HT	0.07**	0.33**	0.13**	0.16**	1.16**	0.15	1.30	-0.522	0.535	-0.444
Snout - upper fin	SU	0.18**	0.25**	0.08*	0.07*	0.48**	0.40	0.89	0.121	0.091	0.110
Number of upper tooth rows	UTR	0.00	0.28**	0.48**	0.41**	1.27**	0.07	1.34	-0.737	0.678	0.661
Number of lower tooth rows	LTR	0.00	0.01	1.52**	0.44**	2.26**	0.28	2.26	-0.009	-0.718	0.609

#### ANALYSIS OF COVARIANCE

With ANCOVA, influence of total length, ecotype, genus, and the interaction between ecotype and genus, were significant for gross body measures with the exception of genus on snout-vent length. The tooth row characters were not influenced by total length; influence of ecotype and the interaction between ecotype and genus were significant for both upper and lower tooth rows, whereas the influence of genus was only significant for the number of upper tooth rows (Table VII).

MANCOVA produced three, linearly dependent, discriminant functions (Table VII). Both ecotypes and genera were best differentiated by number of upper tooth rows but also by height of tail. Number of lower tooth rows only differentiated between ecotypes. For the effect of genus, tooth row characters and height of tail enter with identical signs, whereas, for the effect of ecotype, these variables enter with opposite signs. Interactions were influenced mainly by the tooth row characters with opposite signs, but also by height of tail and snout vent length, both in the same direction with the number of upper tooth rows. Craniad extension of upper fin discriminated only weakly between any factor or interaction (Table VII).

The observed standardized MANCOVA discriminant functions associated with genus, ecotype, and their interaction, condensed the morphometric results. compared with the pooled pond-dwelling species, the pooled phytotelmonous species were characterized by fewer upper and lower tooth rows, while, relative to their total length, they had higher tails. For the pond-dwelling species, higher number of lower tooth rows was found in both genera while higher number of upper tooth rows was found only in *P. venulosa*.

Discrimination in height of tail between ecotypes and genera was influenced mainly by *O. taurinus*, which had the relatively lowest tail, while the tail characteristics of the other species were comparatively uniform.

## DISCUSSION

Tadpoles of both the pond-dwelling and the phytotelmonous species studied are characterized by overall average body dimensions and, thus, resemble typical hyloid pond tadpoles (DUELLMAN, 1970). *P. resinifictrix* and *P. venulosa* larvae are longer, have proportionately longer tails, higher upper tail fins, more lateral eyes, and more anterior nares than *O. oophagus* and *O. taurinus* larvae. As far as known from the literature (see caption of fig. 7), these intergeneric differences in height of tail and position of eyes and nares also apply to the other species of the two genera.

Collectively, buccopharyngeal features of the four species studied represent a relatively uniform type, which we consider omnivorous to macrophagous and capable of both branchial and pulmonary respiration. Nevertheless, number and size of buccopharyngeal papillae, complexity of branchial filter system, development of velar secretory tissues, differentiation of gills, along with number of tooth rows and of labial papillae, correspond to the principal larval habitat types as usual among anuran larvae: relative structural "simplification" characterizes the phytotelmonous larvae, whereas "elaboration" characterizes the pond-dwelling ones (WASSERSUG, 1980; ALTIG & JOHNSTON, 1989).

Less differentiated external and internal buccopharyngeal features along with the more anterior position of the oral disk in the phytotelmonous species are explained by their predominantly macrophagous feeding habits. Among the phytotelm-dwelling species analyzed, however, most internal buccopharyngeal features are less differentiated in *O. oophagus* than in *P. resinifictrix*. This divergence may be explained by different degrees of "specialization" (TRUEB, 1973) to macrophagous nutrition: *O. oophagus* is obligatorily macrophagous, feeding on conspecific fertilized eggs and tadpoles (HÖDL, 1993), while *P. resinifictrix* is omnivorous (GRILLITSCH, 1992; SCHIESARI, 1993), predominantly macrophagous (SCHIESARI, 1993), feeding mainly on conspecific fertilized eggs, but also on detritus (SCHIESARI & GORDO, 1993). Among the pond-dwelling species, buccopharyngeal surface features are more differentiated in *P. venulosa*, indicating a greater reliance on microphagous feeding than in *O. taurinus*. *O. taurinus* larvae have been observed in the field to be voracious egg-eaters (SCHIESARI, personal observation), which matches the morphological indication of macrophagy. *Osteocephalus elkejungingerae*, whose tadpoles are highly cannibalistic when laboratory bred (HENLE et al., 1983), represents a further species within the genus with macrophagous larvae.

Lungs are spacious in the four species analyzed, although more expanded in *Phrynohyas* than in *Osteocephalus*. Comparing among phytotelmonous larvae, glottis and lungs are large in *P. resinifictrix* as in the tree hole-dwelling *Phyllautus* sp. and *Theleiderma stellatum* (WASSERSUG et al., 1981), but are medium sized in *O. oophagus* as in the bromeliad-dwelling *Osteopilus brunneus* (LANNOO et al., 1987). Among the two types of

<p><i>O. buckleyi</i></p>	<p><i>O. elkejungingerae</i></p>	<p><i>O. langsdorffii</i></p>
<p><i>O. oophagus</i></p>	<p><i>O. taurinus</i></p>	<p><i>O. verruciger</i></p>
<p><i>P. mesophaea</i></p>	<p><i>P. resinifictrix</i></p>	<p><i>P. venulosa</i></p>

Fig 7. — Variation of larval tooth row formulae among *Osteocephalus* and *Phrynohyas* species. Schematic drawings; median interruptions and relative lengths of lower tooth rows not considered.

References: *Osteocephalus buckleyi* (HERO, 1990); *Osteocephalus elkejungingerae* (HENLE, 1981); *Osteocephalus langsdorffii* (DUELLMAN, 1974); *Osteocephalus oophagus* (present study and as in Table I); *Osteocephalus taurinus* (present study and as in Table I); *Osteocephalus verruciger* (TRUEB & DUELLMAN, 1970); *Phrynohyas coriacea* (SCHIESARI & MOREIRA, in press); *Phrynohyas mesophaea* (LUTZ, 1973; SCHIESARI, personal observation); *Phrynohyas resinifictrix* (present study and as in Table I); *Phrynohyas venulosa* (present study and as in Table I).

phytotelms, tree holes offer the more anaerobic aquatic environment: dissolved oxygen was 0.2 mg/l (surface water 26°C, 25 l water volume) in tree hole water dwelled by *P. resinifictrix* larvae, but 2.6 mg/l (26°C, 10-15 ml water volume) in the water of bromeliad leaf axils inhabited by *O. oophagus* larvae (SCHIESARI, personal observation). Correspondingly, development of lungs indicates greater importance of pulmonary respiration in tree hole-dwelling larvae than in the bromeliad-dwelling ones, whereas gill development indicates that the contrary applies to branchial respiration. Comparing within a genus, development of internal gills and lungs indicate greater reliance on branchial respiration but also on pulmonary respiration (especially in *O. taurinus*) in the pond-dwelling species. "Internal oral structures of anuran larvae can be used to make reasonably sound predictions about the feeding and respiratory ecology of anuran larvae" (WASSERSUG, 1980). Respiratory structures in the species studied indicate comparatively low average levels of dissolved oxygen also in the larval pond habitats. However, since "lungs appear to be advantageous to aquatic organisms even in normoxic water in that they allow buccopharyngeal surfaces to be dedicated fully to feeding rather than respiration" (WASSERSUG & MURPHY, 1987), extensive development of lungs in the pond-dwelling species studied might further correlate with their less macrophagous, more omnivorous nutrition and, at last, with correspondingly higher motility and metabolic rate in these species which, in contrast to the phytotelmonous ones, develop without "parental" food supply in a, typically, less confined habitat.

For the four species studied, shape of labial keratodonts represents a type very common in Ranoidea tadpoles (e.g., HÉRON-ROYER & VAN BAMBECKE, 1889; GOSNER, 1959; INGER, 1985; ALTIG & JOHNSTON, 1989). Gross jaw sheath morphology shows no considerable peculiarities in the pond-dwelling larvae but is remarkable in the phytotelmonous ones (e.g., DUELLMAN, 1970): edges are smooth in *O. oophagus*, whereas *P. resinifictrix* shows elongate, acutely pointed serration. Smooth edged jaw sheaths are rare in anuran larvae. Among phytotelmonous tadpoles, the upper jaw sheath is smooth and the lower finely serrated in two oophagous species, the bromeliad-dwelling *Hyla zeteki* (DUELLMAN, 1970: 326, first paragraph) and the tree hole-dwelling *Phyllautus* sp. (WASSERSUG et al., 1981); furthermore, in some egg-eating Jamaican hylids, jaw sheaths are not denticulate (NOBLE, 1929). However, some stream-dwelling tadpoles (*Hyla mixe*, *Hyla mixomaculata*) also bear smooth-edged jaw sheaths (DUELLMAN, 1970), and, in contrast, fine uniform jaw sheath serration is frequently reported for phytotelmonous, oophagous larvae (e.g., *Osteopilus brunneus*, LANNOO et al., 1987; *Theloderma stellatum*, WASSERSUG et al., 1981). Thus, various jaw sheath patterns are apparently suitable for oophagous feeding. Smooth-edged jaw sheaths are likely to have different functional correlates in rheophilous and oophagous tadpoles. In rheophilous larvae, smooth jaw sheaths may be most effective for grazing on constrained epilithic substrates; in obligatorily macrophagous oophagous larvae, such as *O. oophagus*, serration simply may have become unnecessary or even disadvantageous for ingesting eggs as a whole.

In the ontogenetic sequence of tooth row appearance, the labial tooth row formula 2/3 is primary in both genera (fig. 7). Additional, secondary upper tooth rows develop in *Phrynohyas* (except in *P. resinifictrix*), where they are added distally. In contrast, they are absent in *Osteocephalus*, with the exception of *O. elkejungingerae*, where they are proximal and poorly formed. Hence, the two genera are well distinguished by different derived types



of ontogenetic tooth row increase (types A to E in ALTIG & JOHNSTON, 1989): in both genera, tooth rows are added centrifugally in the lower labium, but addition of tooth rows in the upper labium is absent (type not considered in ALTIG & JOHNSTON, 1989) or centripetal (type B) in *Osteocephalus* and centrifugal (type C) in *Phrynohyas*. The basic 2/3 tooth row pattern (type A) persists only in the phytotelmonous *O. oophagus* and occasionally in *P. resinificatrix*.

Total numbers of tooth rows of 5 or more than 5, as in *O. oophagus* and in *P. resinificatrix* respectively, compare to the highest known for phytotelmonous hylids (LANNOO et al., 1987). Likewise, among non-phytotelmonous hylids and anuran larvae in general (ALTIG & JOHNSTON, 1986, 1989), total number of tooth rows is comparatively high in all *Osteocephalus* and *Phrynohyas* species (fig. 7): in the pond- and stream-dwelling *Osteocephalus* species, maximum total numbers of tooth rows vary from 7 to 10, which is typical for lotic but not rheophilous hylid tadpoles. Surprisingly, the highest tooth row counts of up to 10 or 11 are present in the evidently lentic *Phrynohyas coriacea*, *P. mesophaea* and *P. venulosa*, as in the pond-dwelling tadpoles of the hylid *Trachycephalus jordani* (MCDIARMID & ALTIG, 1990). These tooth row counts exceed the upper limit of the range of variation known for other lentic hylids, and, furthermore (compared to the data in ALTIG & JOHNSTON, 1986), are within the upper third of the range of variation in lotic hylid tadpoles.

Upper and lower tooth row counts are negatively imbalanced in the two genera studied. Balance values of  $-1$  and  $-2$  as shown in *O. oophagus* and *P. resinificatrix* are moderate among phytotelmonous tadpoles (LANNOO et al., 1987), and represent the most frequent type among hylids as well as among anuran larvae in general (ALTIG & JOHNSTON, 1986, 1989). In all other *Osteocephalus* and *Phrynohyas* species, number of tooth rows in the lower labium exceeds that in the upper labium notably (fig. 7): balance values of  $-3$  to  $-4$  are the most common in the two genera (fig. 7) and in *Osteocephalus* even reach  $-5$  (*O. taurinus*) and  $-6$  (*O. buckleyi*). However, in anurans in general, balance values of  $-3$  to  $-6$  are rare and are most common to lotic larvae (usually neotropical *Hyla* species), though  $-3$  may be also found in phytotelmonous larvae (e.g., *Hyla bromelacea*; DUELLMAN, 1970).

Among hylids, the combination of a wide dorsomedian interruption of the peribuccal papillary margin, as typical for "generalized pond-type" hylid tadpoles (DUELLMAN, 1970), with a number of tooth rows exceeding the typical pond-type 2/3 pattern, is rare and characterizes both *Osteocephalus* and *Phrynohyas*. A wide dorsomedian papillary gap and increased number of lower tooth rows, as is typical in *Osteocephalus*, is known, e.g., in the bromeliad *Hyla dendroscarta* and the pond-dwelling *Hyla rufitela* larvae (DUELLMAN, 1970). A wide dorsomedian papillary gap and increased numbers of both upper and lower tooth rows, as is typical in *Phrynohyas*, is only known in the pond-dwelling tadpoles of *Hyla geographica* (BOKERMAN, 1963; HERO, 1990; RADA DE MARTINEZ, 1990) and *Trachycephalus jordani* (MCDIARMID & ALTIG, 1990). Let us mention here that TRUEB (1970) suggested comparatively close phylogenetic relationship for the genera *Osteocephalus*, *Phrynohyas* and *Trachycephalus*. This proposal based on geographical and adult morphological evidence is supported by larval oral disk morphology and is not contradicted by the other larval features examined in this study.

## SUMMARY AND CONCLUSIONS

Although breeding sites of the species studied in depth are assigned to two principal types (phytotelms and ponds), with discriminant analysis, the external morphological characters analyzed cluster the four species into three distinct groups (fig. 6). The first is the phytotelmonous group with only slight differences between the bromeliad species (*O. oophagus*) and the tree hole habitating species (*P. resinifictrix*), suggesting comparatively little ecological diversity among these species. The other two morphotypological groups are both pond forms (*O. taurinus* and *P. venulosa*), suggesting greater ecological diversity in that habitat.

Among phytotelmonous hylids (as reviewed in LANNOO et al., 1987), external larval morphology assigns both *O. oophagus* and *P. resinifictrix* to a relatively "generalized" (TRUEB, 1973) larval type in that they show "typical pond tadpole" (LANNOO et al., 1987) body proportions, and oral disk features similar to those phytotelmonous species which feed mainly on detritus. For both species analyzed, dietary information and buccopharyngeal morphology indicate predominating oophagous, carnivorous macrophagy, reduced microphagy, and branchial as well as pulmonary respiration with evidently greater reliance on generalized diet in *P. resinifictrix*. For *P. resinifictrix*, LANNOO et al. (1987) therefore stated that "they appear restricted to larger aquatic bodies, which are more likely to occur in tree holes than in leaf axils". *P. resinifictrix*, in fact, is exclusively known to breed in spacious tree holes (Table VIII). Comparatively high degree of morphological congruency of *P. resinifictrix* and *O. oophagus* corresponds to their collectively relatively low degree of "specialization" (TRUEB, 1973), which, for *O. oophagus*, may be explained by its remarkable flexibility in breeding habitat selection: although typically breeding in bromeliads, this species has also been reported to breed in other, considerably diverse water-filled plant structures (Table VIII).

For the non-phytotelmonous larvae of the two genera, data from the literature on external larval morphology of other species greatly match the intergeneric differences observed in the species studied in depth in this study. Collectively, comparatively high tail fins, lateral eyes, and balanced tooth row formulae, as in *Phrynohyas*, are typical for nektonic lentic tadpoles, while the opposite, as shown by *Osteocephalus*, is typical for benthic, commonly moderately lotic larvae. Data compiled from the literature on breeding habitats of non-phytotelmonous congeners (Table VIII) apparently parallel the above morphotypological grouping: all *Phrynohyas* species regularly breed in ponds, whereas *Osteocephalus* larval habitats comprise lentic, and facultatively as well as permanently lotic habitats. Most of the *Osteocephalus* species, in fact, breed in a stream habitat.

However, total number of tooth rows in the lentic *Phrynohyas* species matches or exceeds that of the most lotic *Osteocephalus* species, and, thus, corresponds to habitat inversely than usual among anuran larvae. Furthermore, compared to typical pond-type larvae, tooth row counts are unusually high and balance values are unusually low at least in the non-phytotelmonous species of both genera, more like in lotic rather than in lentic tadpoles. Our observations might be paralleled in other groups of neotropical hylids. WASSERSUG (1980) found a mosaic of stream and pond related features in the

Table VIII. - Literature survey on breeding habitats of the *Osteocephalus* and *Phrynohyas* species with information on larval external morphology available (fig. 7) Regions refer to the sites of observation and do not necessarily cover the species' entire range of distribution.

Species	Principal habitat types			Habitats		Regions	References
	Stream	Pond	Phytotem				
<i>O. buckleyi</i>	+	-	-	Small streams	Primary forest	Central and upper Amazon basin (Brasil, Perú)	HERO (1990); HÖDL (1990, 1993); RODRIGUEZ & DUELLMAN (1994)
<i>O. eikejungingeriae</i>	+	-	-	Small, shallow, slowly to moderately fast flowing waters	Forest	Lower eastern Andean slopes (Perú)	HENLE (1981), HENLE et al. (1983); HENLE (1992)
<i>O. langsdorffi</i>	-	+	-	Temporary ponds	Forest-border	Atlantic forest (Brasil)	DUELLMAN (1974), FROST (1985), SCHIESARI (pers. obs.)
<i>O. oophagus</i>	-	-	+	Epiphytic or ground bromeliads, palm leaf axils, palm bracts lying in the ground, tree holes up to about 35 m high, plastic basins on the ground	Primary and secondary forest	Central Amazon basin (Brasil)	JUNGER & SCHIESARI (1995); JUNGER & WEYGOLDT (1995)
	-	-	+	Leaf axils in arboreal plants, bromeliads, palm leaf axils, equivalent arboreal plant structures	Forest	Central Amazon basin (Brasil)	HERO (1990), HÖDL (1990, 1993) <sup>1</sup>
<i>O. species</i>	-	-	+	Bromeliads	Primary forest	Upper Amazon basin (Perú)	RODRIGUEZ & DUELLMAN (1994)
<i>O. laurinus</i>	+	+		Large and small, temporary and permanent ponds, streamside ponds and isolated forest ponds, large and small streams, in forest and forest-edge sites	Primary and secondary forest	Central and upper Amazon basin (Brasil, Perú)	BOKERMANN (1964); HERO (1990); HÖDL (1990, 1993); ZIMMERMAN & RODRIGUEZ (1990), GASCON (1991, 1993); RODRIGUEZ & DUELLMAN (1994)
<i>O. verruciger</i>	+	-	-	Quiet pool in a stream	Humid montane forest	Lower eastern Andean slopes (Ecuador)	TRUEB & DUELLMAN (1970, 1971)
<i>P. coriacea</i>	-	+	-	Temporary ponds	Primary forest	Central and Upper Amazon basin (Brasil, Perú)	HÖDL (1990, 1993), RODRIGUEZ & DUELLMAN (1994), SCHIESARI & MOREIRA (in press)
<i>P. mesophaea</i>	-	+	-	Temporary ponds	-	Atlantic forest (Brasil)	FROST (1985); SAZIMA (1974)
<i>P. resiniferus</i>	-	-	+	Spacious cavities high in large trees	Primary forest	Amazon basin (Brasil, Perú)	References in ZIMMERMAN & HÖDL (1983), HERO (1990, 1991); GRILLITSCH (1992), HÖDL (1993); SCHIESARI (1993); RODRIGUEZ & DUELLMAN (1994)
<i>P. venulosa</i>	-	+	-	Shallow temporary ponds	Open, nonforested but also primary and secondary forest sites	Neotropical lowlands	References in ZIMMERMAN & HÖDL (1983), RODRIGUEZ & DUELLMAN (1994)

1. Described under the name *Osteocephalus* sp (W. HÖDL, personal communication)

bromeliad-dwelling *Hyla dendroscarta* tadpoles. Within species, closely related to *H. dendroscarta*, he recognized a variety of breeding habitats, which, as in the genera *Osteocephalus* and *Phrynohyas*, comprise ponds, streams, and phytotelms.

In summary, *Osteocephalus* and *Phrynohyas* larval habitats are notably diverse. But morphologically, larvae among the two genera are less diverse in that they share similar oral disk and buccopharyngeal features as well as overall average body proportions, high number of tooth rows, low balance values, omnivorous to macrophagous diets, and branchial as well as pulmonary respiration. Particularly, number of tooth rows and lung development do not correspond to habitat in the usual anuran larval fashion.

Two, not mutually exclusive, biological explanations for the generally high number of tooth rows and the well developed lungs in the extant non-phytotelmonous species examined are possible.

(1) Adaptation to contemporary environment. - Their contemporary larval environment is collectively characterized by comparatively high temperatures and correspondingly low oxygenation. If aerial respiration is the expected major factor in the development of lungs (as reviewed in WASSERSUG & SEIBERT, 1975 and WASSERSUG & MURPHY, 1987), low levels of dissolved oxygen favor early and extensive development of lungs in lentic but also in lotic tadpoles (NOBLE, 1929). If adhesion to substrate is the expected major action among the suggested functions of labial teeth (as reviewed in ALTIG & JOHNSTON, 1989), increased number of tooth rows, i.e., increased adhesive efficiency of the oral disk, might be an adaptation to compensate the hydrodynamic disadvantage (NOBLE, 1929; WASSERSUG, 1980) of well developed lungs especially in lotic environments. This explanation is more likely to apply to the lotic benthic *Osteocephalus* species than to the lentic nektonic *Phrynohyas* species. For both genera, increase in adhesive capacity of oral disk might also be a not yet considered correlate to macrophagous nutrition.

(2) Persistent influence of ancestral patterns. - Some features, such as high number of tooth rows in the lentic species, might represent an ancestral lotic pattern and might have persisted relatively unchanged. If breeding in phytotelms is "derived" (TRUEB, 1973) in the genera studied, other features, such as pulmonary respiration and omnivorous, predominantly macrophagous nutrition in non-phytotelmonous larvae, might further be exaptations (GOULD & VRBA, 1982) to life in lowly oxygenated and "confined" (e.g., LANNON et al., 1987) phytotelmonous habitats.

## RESUMEN

La morfología externa y bucofaringea de larvas habitantes de fitotelmata y charcos de cuatro especies de hildos neotropicales fueron analizadas con relación a diagnosis diferencial y ecomorfología. Los hábitats larvales típicamente comprenden bromelias (*Osteocephalus oophagus*), hoquedades en árboles (*Phrynohyas resinifictrix*), charcos en áreas de selva (*Osteocephalus taurinus*) y charcos en áreas abiertas (*Phrynohyas venulosa*). Un análisis discriminante de caracteres externos morfométricos reveló dos subgrupos ligeramente diferentes dentro del grupo de habitantes de fitotelmata pero dos subgrupos bien separados dentro del grupo de los habitantes de charcos. Todas las especies

mostraron proporciones corporales del tipo de un renacuajo generalista, hábitos macrófagos y respiración tanto branquial como pulmonar. Los renacuajos que viven en fitotelmata fueron caracterizados por la reducción de las estructuras peribucales y bucofaríngeas, y difirieron marcadamente en la morfología del pico córneo y en el desarrollo de los pulmones. Los renacuajos que se desarrollan en charcos fueron caracterizados por un alto número de filas de denticulos y por valores de balance bajos. Los géneros *Phrynohyas* y *Osteocephalus* se distinguieron mejor por el desarrollo de filas de denticulos superiores secundarias, por la posición de los ojos y por las proporciones corporales groseras.

#### ACKNOWLEDGEMENTS

We are indebted to the University of Vienna for funding this research (Scientific Exchange Program between the University of São Paulo and the Faculty of Natural Sciences, University of Vienna) as well as to the support of the University of Veterinary Medicine of Vienna W HÖDL initiated and promoted our cooperation. M. GORDO helped in the collection of *P. resinificatrix* larvae, T. LOSERT in SEM techniques, K. REPP in preparation of drawings, and R. WYTEK in statistical analyses. G. SKUK translated the Spanish resumen. H. GRILLITSCH, A. C. MARQUES and H. L. NEMESCHKAL provided discussion and valuable advice. L. C. SCHIESARI expresses his gratitude to Eva and Angelika RIEDER for hospitality in Vienna. We graciously acknowledge R. WASSERSUG for review and constructive advice.

#### LITERATURE CITED

- ALTIG, R. & JOHNSTON, G. F., 1986. — Major characteristics of free-living anuran tadpoles. *Smithson. herpet. Inf. Serv.*, **67**: 1-75.
- 1989. — Guilds of anuran larvae: relationships among developmental modes, morphologies, and habitats. *Herpet. Monogr.*, **3**: 81-109.
- BOKERMAN, W. C. A., 1963. — Girinos de anfíbios brasileiros. I (Amphibia - Salientia). *An. Acad. bras. Ciênc.*, **35**: 465-474.
- CALDWELL, J. P., 1989. — Structure and behavior of *Hyla geographica* tadpole schools, with comments on classification of group behavior in tadpoles. *Copeia*, **1989**: 938-950.
- DUBOIS, A., 1995. — Keratodont formulae in anuran tadpoles. proposals for a standardization. *J. zool. Syst. evol. Res.*, **33**: I-XV
- DUELLMAN, W. E., 1970. — The hylid frogs of Middle America. *Monogr. Mus. nat. Hist. Univ. Kansas*, **1** (1) i-xi + 1-427; **1** (2): 429-753, pl. 1-72.
- 1974. — A reassessment of the taxonomic status of some neotropical hylid frogs. *Occas. Pap. Mus. nat. Hist. Univ. Kansas*, **27**: 1-27.
- 1978. — The biology of an equatorial herpetofauna in Amazonian Ecuador. *Univ. Kansas Mus. nat. Hist. misc. Publ.*, **65**: 1-352, pl. 1-4.
- 1988. — Patterns of species diversity in anuran amphibians in the American tropics. *Ann. Missouri bot. Gard.*, **75**: 79-104.
- DUELLMAN, W. E. & LESCURE, J., 1973. — Life history and ecology of the hylid frog *Osteocephalus taurinus*, with observations on larval behavior. *Occas. Pap. Mus. nat. Hist. Univ. Kansas*, **13**: 1-12.
- DUELLMAN, W. E. & TRUEB, L., 1985. — *Biology of amphibians*. New York, McGraw-Hill: i-xix + 1-670.

- FOX, H., 1984. — *Amphibian morphogenesis* Clifton N.J., Humana Press: 1-xv + 1-301.
- FROST, D. R. (ed), 1985 — *Amphibian species of the world*. Lawrence, Allen Press & Assoc. Syst. Coll.: [i-iv] + i-v + 1-732.
- GASCON, C., 1991 — Population- and community-level analyses of species occurrences of central Amazonian rainforest tadpoles. *Ecology*, **72**: 1731-1746.
- GASCON, K. L., 1993 — Breeding-habitat use by five Amazonian frogs at forest edge. *Biodivers. Conserv.*, **2**: 438-444.
- GOSNER, K. L., 1959. — Systematic variations in tadpole teeth with notes on food. *Herpetologica*, **15**: 203-210
- 1960. — A simplified table for staging anuran embryos and larvae, with notes on identification. *Herpetologica*, **16**: 183-190.
- GOULD, S. J., 1966. — Allometry and size in ontogeny and phylogeny. *Biol. Rev.*, **41**: 587-640.
- GOULD, S. J. & VRBA, E. S., 1982 — Exaptation - a missing term in the science of form. *Paleobiology*, **8**: 4-15.
- GRILLITSCH, B., 1992. — Notes on the tadpole of *Phrynohyas resinificatrix* (Goeldi, 1907) Buccopharyngeal and external morphology of a tree hole dwelling larva (Anura: Hylidae). *Herpetozoa*, **5**: 51-66.
- GRILLITSCH, B., GRILLITSCH, H., DUBOIS, A. & SPLECHTNA, H., 1993 — The tadpoles of the brown frogs *Rana [graeca] graeca* and *Rana [graeca] italica* (Amphibia, Anura). *Alytes*, **11**: 117-139
- HENLE, K., 1981 — *Hyla elkejungingerae*, ein neuer Hylide aus dem peruanischen Regenwald (Amphibia: Salientia: Hylidae). *Amphibia-Reptilia*, **2**: 123-132.
- 1992. — Zur Amphibienfauna Perus nebst Beschreibung eines neuen *Eleutherodactylus* (Leptodactylidae). *Bonn. zool. Beitr.*, **43**: 79-129.
- HENLE, K., EHRL, A. & PILGRAM, C., 1983 — Zum Biotop und zur Aufzucht des peruanischen Laubfrosches *Hyla elkejungingerae* Henle 1981. *Herpetofauna*, **24**: 8-9.
- HERO, J.-M., 1990 — An illustrated key to the tadpoles occurring in the central Amazon rainforest, Manaus, Amazonas, Brasil. *Amazoniana*, **11**: 201-262.
- HÉRON-ROYER & VAN BAMBEKE, C., 1889. — Le vestibule de la bouche chez les têtards des batraciens anoures d'Europe, sa structure, ses caractères chez les diverses espèces. *Arch. Biol.*, **9**: 185-309, pl. 12-24.
- HÖDL, W., 1990. — Reproductive diversity in Amazonian lowland frogs. In: W. HANKE (ed.), *Biology and physiology of amphibians*, *Fortschr. Zool.*, **38**: 41-60
- 1993. — Amazonien aus der Froschperspektive. Zur Biologie der Frösche und Kroten des Amazonastieflandes. *Kataloge OÖ. Landesmus.*, (N. F.), **61**: 499-545.
- INGER, R. F., 1985. — Tadpoles of the forested regions of Borneo. *Fieldiana: Zool.*, (n.s.), **26** i-v + 1-89
- JOHNSON, R. A. & WICHERN, D. W., 1988. *Applied multivariate statistical analysis*. London, Prentice-Hall: i-xii + 1-640.
- JUNGER, K.-H. & SCHIESARI, L. C., 1995. — Description of a new central Amazonian and Guianan treefrog, genus *Osteocephalus* (Anura, Hylidae), with oophagous tadpoles. *Alytes*, **13**: 1-13.
- JUNGER, K.-H. & WEYGOLDT, P., 1995. — Reproductive biology of the central Amazonian frog *Osteocephalus oophagus* *Abstracts 8th O G M Societas Europaea Herpetologica, Bonn, 1995*: 69.
- KAUNG, H. L. C. & KOLLROS, J. J., 1976. — Cell turnover in the beak of *Rana pipiens*. *Anat. Rec.*, **188**: 361-370.
- LANNOO, M. J., TOWNSEND, D. S. & WASSERSUG, R. J., 1987. — Larval life in the leaves: arboreal tadpole types, with special attention to the morphology, ecology, and behavior of the oophagous *Osteopilus brunneus* (Hylidae) larva. *Fieldiana, Zool.*, (n. s.), **38**: 1-31.
- LUTZ, B., 1973. *Brazilian species of Hyla* Austin & London, University of Texas Press: i-xix + 1-265, pl. 1-7.
- MCDIARMID, R. & ALTIG, R., 1990. — Description of a bufonid and two hylid tadpoles from western Ecuador. *Alytes*, **8**: 51-60.
- MORRISON, D. F. 1990. — *Multivariate statistical methods* New York, McGraw-Hill: 1-xvii + 1-493.
- NOBLE, G. K., 1929. — The adaptive modifications of the arboreal tadpoles of *Hoplophryne* and the torrent tadpoles of *Stauroids*. *Bull. amer. Mus. nat. Hist.*, **58**: 291-334.

- PYBURN, W. F., 1967. — Breeding and larval development of the hylid frog *Phrynohyas spilomma* in southern Veracruz, Mexico. *Herpetologica*, **23**: 184-194.
- RADA DE MARTINEZ, D., 1990. — Contribución al conocimiento de las larvas de anfibios de Venezuela. *Mem. Soc. Cienc. nat. La Salle*, **50**: 391-403.
- RODRÍGUEZ, L. O. & DUELLMAN, W. E., 1994. — Guide to the frogs of the Iquitos region, Amazonian Peru. *Univ. Kansas nat. Hist. Mus. Special Publ.*, **22**: 1-80.
- SAZIMA, I., 1974. — An albino hylid frog, *Phrynohyas mesophaea* (Hensel) *J. Herpet.*, **8**: 264-265.
- SCHIESARI, L. C., 1993. — Estudio da morfologia da larva de *Phrynohyas resinificatrix* (Anura, Hylidae) *3º Congr. Lat.-Amer. Herpet.*, 1993: 144.
- SCHIESARI, L. C. & GORDO, M., 1993. — Aspectos da história natural do Canauarú, *Phrynohyas resinificatrix* (Anura, Hylidae). *3º Congr. Lat.-Amer. Herpet.*, 1993: 143.
- SCHIESARI, L. & MOREIRA, G., in press. — The tadpole of *Phrynohyas coriacea* (Peters, 1867) (Anura: Hylidae), with comments on the species' reproduction. *J. Herpet.*, in press.
- SHAW, R. G., 1987. — Maximum-likelihood approaches applied to quantitative genetics of natural populations. *Evolution*, **41**: 812-826.
- SWALLOW, W. H. & MONAHAN, J. F., 1984. — Monte Carlo comparison of ANOVA, MIVQUE, REML, ML estimators of variance components. *Technometrics*, **26**: 47-57.
- TRUEB, L., 1970. — Evolutionary relationships of casque-headed treefrogs with co-ossified skulls (family Hylidae). *Univ. Kansas Publ. Mus. nat. Hist.*, **18**: 547-716.
- 1973. — Bones, frogs, and evolution. In: J. L. VIAL (ed.), *Evolutionary biology of the anurans*, Columbia, Univ. Missouri Press: 65-132.
- TRUEB, L. & DUELLMAN, W. E., 1970. — The systematic status and life history of *Hyla verrucigera* Werner. *Copeia*, **1970**: 601-610.
- 1971. — A synopsis of neotropical hylid frogs, genus *Osteocephalus*. *Occas. Pap. Mus. nat. Hist. Univ. Kansas*, **1**: 1-47.
- VIERTEL, B., 1982. — The oral cavities of central European anuran larvae (Amphibia). Morphology, ontogenesis and generic diagnosis. *Amphibia-Reptilia*, **4**: 327-360.
- WASSERSUG, R., 1976. — Oral morphology of anuran larvae: terminology and general description. *Occas. Pap. Mus. nat. Hist. Univ. Kansas*, **48**: 1-23.
- 1980. — Internal oral features of larvae from eight anuran families: functional, systematic, evolutionary and ecological considerations. *Univ. Kansas Mus. nat. Hist. misc. Publ.*, **68**: 1-146.
- WASSERSUG, R. J., FROGNER, K. J. & INGER, R. F., 1981. — Adaptations to life in tree holes by rhacophorid tadpoles from Thailand. *J. Herpet.*, **15**: 41-52.
- WASSERSUG, R. & HEYER, W. R., 1988. — A survey of internal oral features of leptodactyloid larvae (Amphibia: Anura). *Smithson. Contrib. Zool.*, **457**: 1-19 + 1-99.
- WASSERSUG, R. J. & MURPHY, A. M., 1987. — Aerial respiration facilitates growth in suspension-feeding anuran larvae (*Xenopus laevis*). *Exper. Biol.*, **46**: 141-147.
- WASSERSUG, R. J. & SEIBERT, E. A., 1975. — Behavioral responses of amphibian larvae to variation in dissolved oxygen. *Copeia*, **1975**: 86-103.
- ZIMMERMAN, B. L. & HÖDL, W., 1983. — Distinction of *Phrynohyas resinificatrix* (Goeldi, 1907) from *Phrynohyas venulosa* (Laurenti, 1768) based on acoustical and behavioural parameters (Amphibia, Anura, Hylidae). *Zool. Anz.*, **1983**: 341-352.
- ZIMMERMAN, B. L. & RODRIGUES, M. T., 1990. — Frogs, snakes, and lizards of the INPA-WWF reserves near Manaus, Brazil. In: A. H. GENTRY (ed.), *Four neotropical rainforests*, New Haven & London, Yale University Press. 426-454.
- ZWEIFEL, R. G., 1964. — Life history of *Phrynohyas venulosa* (Salicentia: Hylidae) in Panamá. *Copeia*, **1964**: 201-208.

Corresponding editor: Alain DUBOIS.